

Herp.

19785

Herp.

QL  
666  
.0636  
F47  
2001

# Scientific Papers

MCZ  
LIBRARY

AUG 06 2001

HARVARD  
UNIVERSITY

Natural History Museum  
The University of Kansas

15 June 2001

Number 19:1-6

## Further Study of the Garter Snake, *Thamnophis sirtalis*, in Northeastern Kansas

By

HENRY S. FITCH

Fitch Natural History Reservation, The University of Kansas  
2060 East 1600 Road, Lawrence, Kansas 66044-9450, USA

### CONTENTS

ABSTRACT .....	1
INTRODUCTION .....	2
ACKNOWLEDGMENTS .....	2
MATERIALS AND METHODS .....	2
RESULTS .....	2
DISCUSSION .....	5
LITERATURE CITED .....	6

**ABSTRACT** The red-sided garter snake, *Thamnophis sirtalis parietalis*, is a prominent member of the local snake fauna at the Fitch Natural History Reservation and has been a subject of field study over the past 53 years. Although several publications in whole or in part, have been devoted to this species, some aspects of its ecology have remained poorly known; some of these are dealt with in the present paper. Herein, I discuss the range of variation in color and pattern, and compare the frequencies of pattern types in males and females; I also compare the sexes with each other and with immatures in their ecological traits including vagility and their fidelity to specific locations. Comparison of feeding records show major differences in food habits between the sexes and between young and adults. A northern population of this same subspecies in the Interlake Region in Manitoba, Canada, is compared behaviorally with the Kansas population on the basis of recent studies.

**KEY WORDS:** Dorsolateral area; Funnel trap; Intersquamal color; Probability of capture; *Thamnophis sirtalis parietalis*.

## INTRODUCTION

The common garter snake, *Thamnophis sirtalis*, is ecologically important and geographically widespread; it occurs throughout most of the United States (except the arid southwestern one-fourth) and in the southern half of Canada (Ruthven, 1908). A large amount of literature exists regarding its local occurrence, identification, and interactions with other species (Fitch, 1980). It is in fact one of the best known of North American snakes. The recent book by Rossman et al. (1996) summarizes much information concerning the species. My acquaintance with the species began with studies of the west coast garter snakes at the University of California's Museum of Vertebrate Zoology in the 1930s. (Fitch, 1941). With my becoming the first superintendent of the University of Kansas Natural History Reservation in 1948, I had opportunity to study a local population of the red-sided garter snake (*Thamnophis sirtalis parietalis*) and subsequently published an ecological study on that snake (Fitch, 1965). In that study the population on the Reservation was compared with that in Harvey County State Park, 140 miles to the southwest; geographic variation over the entire range was discussed, and the two local populations were compared with respect to habitat, temperature relationships, food habits, breeding,

growth, movements, defense and escape, natural enemies, parasites, composition of the population and numbers. In my synthesis of a Kansas snake community (Fitch, 1999), I presented data on the common garter snake dealing with traits of the species, behavior, size relationships, pattern types, tail functions, spatial relationships, kinds of prey, reproduction, growth, numbers, and geographic differentiation. Since that study was completed, three more seasons of field work on garter snakes have been finished. The present report deals with aspects of the ecology not undertaken or adequately treated in previous publications, to describe in detail the color pattern phases and their incidence in a large sample, and to compare the sexes with each other and with immatures in their ecological traits.

## ACKNOWLEDGMENTS

I thank William E. Duellman for his advice regarding the content and organization of this paper. I am indebted to Neil B. Ford and Stevan J. Arnold for their many helpful suggestions. My daughter, Alice F. Echelle, helped me with various phases of the early field work and also made suggestions for improving the original manuscript. Also, I thank the many students who have helped me capture snakes over the past 53 years.

## MATERIALS AND METHODS

Garter snakes were captured in wire funnel traps, or by hand from beneath shelters, both metal and wooden, and these contrasting techniques were used on different areas. Data routinely recorded from each snake captured included sex, snout-vent length, tail length, color and markings, and stomach contents. Color pattern was described with special attention to the vertebral stripe, the dark dorsolateral area, and the series of pale intersquamal marks on the body. Lincoln Index censuses were made from time to time on relatively small and discrete areas of intensive study. Each census was based on two consecutive sampling periods; the ratio of marked snakes (from the first sampling) to unmarked snakes in the second sampling was the basis for an estimate; it was obvious that the snakes' movements prevented a highly accurate census, and the longer the sampling period the more distorted the census figure, because previously marked snakes wan-

dered away and were replaced by new ones. Food habits were studied by palping food items from the stomach up into the mouth for identification, and comparisons involved male and female snakes, adults versus first-year young, areas of different habitats and changes over time.

Areas of most intensive study on Fitch Natural History Reservation (FNHR) included House Field (10 ha in the headquarters area sampled from shelters in the 1990s), and Quarry Field (a 3.36 ha hilltop field on the northern edge of the reservation). On the adjacent Nelson Environmental Study Area (NESA), study areas included the Electric Mouse Pens (in the northwestern sector, 9.65 ha sampled with traps in the 1990s), the Fish Pond Pens (2.6 ha south of NESA headquarters, sampled with traps in the 1990s), and Plots 4 and 5 in the southeastern part of the Biotic Succession Area (5.0 ha, sampled with shelters, 1986-2001).

## RESULTS

**Color pattern.**—*Thamnophis sirtalis* has a longitudinally striped pattern, and is one of the most brightly colored snakes. There is much variation, both geographic and individual, in color and pattern, but ontogenetically there is little change, which involves a brightening from the rather dull color of the neonate. Between the scales on loose skin of the dorsolateral area are the colored marks that give the subspecies its vernacular name "red-sided." These

marks are not always red and are highly variable in size and color, providing a variety of pattern types. Table 1 shows the relative frequency of nine pattern types in the local population and shows differences between the sexes. Actually, individual variation is such that a continuum might be established among all nine types. The intersquamal marks are arranged in transverse alternating series, with the two lower rows and the three upper

Table 1. Pattern variation in intersquamous marks of dorsolateral area in a local population of *Thamnophis sirtalis parietalis*. Numbers are percentages of total sample size for each sex (669 males, 1029 females).

Intersquamous pattern	Males	Females
All red	26.5	34.5
All yellow	5.5	3.5
All green	3.9	2.7
All blue	3.2	1.2
Uppermost row pale (russet, ivory, green, or blue)	19.0	14.9
Two upper rows pale	26.5	26.6
Three upper rows pale	12.7	9.1
Four upper rows pale	2.5	2.3
Two upper rows missing ( <i>T. s. fitchi</i> pattern)	0.1	0.2

offset and alternating, separated by about the length of one scale from the next in front or behind. The lowest row is just above the lateral stripe and its marks are the largest; those marks farther from the lateral stripe become progressively smaller and less colorful. The two lower marks are on each side of the fourth scale row; the three upper marks involve scales of the fifth, sixth, and seventh rows. These marks on the dorsolateral area are sometimes all one color (in both sexes combined, 26.3% red, 3.6% yellow, 2.5% green, 2.2% blue), but in some cases only the lower rows are red, and the upper (four, three, two or one) are paler, faintly yellow, green or blue. In occasional individuals, the upper series (two or three nearest the dorsal stripe) are missing, and these snakes have essentially the pattern of the West Coast subspecies, *Thamnophis sirtalis fitchi*. In the majority of local snakes, the upper marks are not red but are pale, ivory, or delicately tinted with yellow, green, or blue. In a small minority, there is no red in the pattern and all dorsolateral marks are of pale color.

Table 2. Relative probability of capture of the red-sided garter snake.

Area	Method of capture	Sex	Total	Number of captures			
				Twice		Three times	
				N	%	N	%
House Field	Under shelters or by hand	♂	175	76	43.4	16	9.1
		♀	184	103	56.0	75	38.7
Biotic Succession Area	Under shelters or by hand	♂	46	5	10.9	1	6.5
		♀	93	24	25.8	11	11.8
Nelson Environmental Study Area	Wire funnel traps	♂	140	35	25.0	15	10.7
		♀	140	50	35.7	20	14.3
Quarry	Wire funnel traps	♂	35	10	28.6	8	22.9
		♀	51	30	58.8	17	33.3
Hilltop outcrop	Wire funnel traps	♂	53	3	6.0	—	—
		♀	81	5	6.3	1	1.3
Reservation, 1950s & 1960s	Wire funnel traps	♂	457	48	10.5	10	2.2
		♀	635	94	14.8	23	3.6

The yellow vertebral stripe is perhaps the most characteristic trait of the species, but in the local population it also is subject to much individual variation. Typically the stripe is bright yellow and involves the vertebral scale row and half of the adjacent row on each side, but it may be a dull, muddy yellow, may be broader than the typical one and two halves of scale rows, and may have indistinct edges. The dorsolateral area between the vertebral stripe and the lateral stripe on each side is typically sepia-colored or almost black, but may be paler brown or gray, with two alternating rows of darker spots and five pairs of transverse markings, largely confined to the skin between the scales.

**Movements and abundance.**—Behavioral differences between the sexes affect their relative probability of capture (Table 2). For example, site fidelity is more prominent in females. This is illustrated by attempts to apply a Lincoln Index census to the data. In 1998 in House Field, snakes were captured exclusively by hand. There were 43 males and 55 females (excluding the young born in late summer). Of the 98 snakes in the sample, 57 were caught in the first half of the season (March, April, May, June), 41 were caught in the latter part (July through October) and 10 of these were captured in both early and late periods. From the ratio of recaptures in late summer and fall the Lincoln Index indicates a population of approximately 234. But if the census is applied separately to males and females, the figures for females are 38 for the first half of the season, 17 for the second half, and 8 for both, with the equation indicating a population of 80.8 individuals. For males, the corresponding figures are 19, 24 and 2, suggesting a population of 228 individuals. Intuitively, it seems that the figure for males is much too high, and is the result of only two recaptures, because most of those present in spring and early summer had moved away by the time of the late summer-fall sampling. Censusing from the ratio of marked to unmarked snakes assumes there is no movement to or from

Table 3. Distances between capture points and implied areas of activity for male, female, and young red-sided garter snakes.

	Males	Females	Young
N	147	398	106
Mean distances (m) between capture points	117.9	116.3	80.6
Implied area (ha)	3.77	3.67	2.23
Recaptures reflecting no net movement	9	44	13

a study area. However, there is always some movement, depending on the length of time involved. In male garter snakes movement is especially prominent, and it is essential to have short sampling periods in order to minimize the effect (Fitch, 1999) and to be aware of the error caused by movement. Compared with females, adult males move farther and more frequently, and they have less tendency to return to any specific location. Therefore, they are less susceptible to recapture, and this affects the ratios in Lincoln Index censuses.

Table 3 shows differences between the sexes and between adults and young in distances moved. The young were all first-year individuals, but most had made substantial growth before their first capture. They were mostly in the range of 300-400 mm in snout-vent length, and thus had about doubled in length since birth. In these partly grown young, the average movements were substantially less than in adults of either sex. It is believed that even smaller young, down to the size of neonates would show progressively shorter movements and their home ranges would be progressively smaller. Adults of both sexes are similar in their movements compared with young, which move within smaller areas. Adult females and young are alike (but differ from males) in their tendency to return frequently to favored spots.

Table 4. Prey of the red-sided garter snake in four areas of the Fitch Natural History Reservation (FNHR) and Nelson Environmental Study Area (NESA) comparing sexes, mean snout-vent lengths in mm (SVL  $\pm$  1 SE), and numbers (N) of snake predators. BSA = Biotic Succession Area of NESA.

Prey	Sex	House Field 1980-2000		FNHR 1950-1990		BSA 1986-2000		NESA Pens 1986-2000	
		N	SVL	N	SVL	N	SVL	N	SVL
Earthworm	♂	54	397.9 $\pm$ 12.1	9	517.7	2	356	—	—
	♀	81	430.6 $\pm$ 11.3	4	475.8 $\pm$ 21.1	6	480.8 $\pm$ 16.9	1	517
<i>Microtus</i>	♂	—	—	—	—	—	—	—	—
	♀	1	623	3	675	6	649.3 $\pm$ 32.7	6	705.7 $\pm$ 21.5
Other mammals*	♂	—	—	1	490	—	—	—	—
	♀	4	600.8 $\pm$ 28.8	10	636.4 $\pm$ 3.14	1	783	4	612.3 $\pm$ 8.8
<i>Rana</i> *	♂	12	496.3 $\pm$ 1.5	15	488.9 $\pm$ 2.5	1	540	6	536.7 $\pm$ 6.2
	♀	23	567.6 $\pm$ 4.3	21	549.0 $\pm$ 6.7	4	669.3 $\pm$ 14.4	27	623.0 $\pm$ 13.8
<i>Bufo</i> *	♂	3	438.6	6	403.3 $\pm$ 0.65	—	—	2	374.0
	♀	3	582.4	7	615.3 $\pm$ 6.2	4	673.0 $\pm$ 18.5	1	745
Other amphibians*	♂	3	354.5	4	364.8 $\pm$ 14.1	4	442.5 $\pm$ 74.2	3	338.3
	♀	9	442.2	7	562.4 $\pm$ 10.0	5	532.6 $\pm$ 12.1	9	591.4 $\pm$ 3.9

\* "Other mammals" includes *Peromyscus*, *Reithrodontomys*, *Blarina*, and *Cryptotis*. "Rana" includes *R. blairi* and *R. catesbeiana*. "Bufo" includes *B. americanus* and *B. woodhousii*. "Other amphibians" includes *Acris*, *Hyla*, *Pseudacris*, and *Gastrophryne*.

On the FNHR until the 1980s, and at the pens area in the NESA, samples of snakes were obtained with wire funnel traps and consisted almost entirely of adults, because immatures easily pass through the quarter-inch wire mesh of the funnel traps. In the Biotic Succession Area (BSA) of the NESA and FNHR in the late 1980s and 1990s, sampling was accomplished by distributing wooden and metal shelters, which presumably were used by snakes of all sizes and ages indiscriminately, but young were relatively few in the upland habitat of the BSA.

**Food habits.**—Studies of food habits have shown major geographic differences within the species but usually have not compared food of the sexes, or compared adults and young. In the local population such differences exist and are shown in Tables 4 and 5. Table 4 shows the total food sample divided into 48 categories to bring out differences between the sexes, between adults and young, and between areas of different habitats.

There are striking differences between areas. The many young captured in House Field had eaten earthworms almost exclusively. One had eaten a small slug (*Deroceras laeve*) and several had eaten newly metamorphosed hylids (*Acris* and *Pseudacris*). Another important difference was predation on small mammals by adult females (30 records, 16 of them on *Microtus ochrogaster*) compared with only one record for a male snake, which had eaten an individual of the much less bulky *Reithrodontomys megalotis*.

Frogs (*Rana blairi* and *R. catesbeiana*) made up a major part of the food and were well represented in each localized sample. *Rana blairi* was eaten about twice as often as *R. catesbeiana*, and none of the latter species was much more

Table 5. Prey eaten by red-sided garter snakes on the FNHR and adjoining areas and sizes of snake predators. In columns of SVL, the first line is the observed range and the second line is the mean  $\pm$  1 SE. Measurements in mm.

Kind of prey*	N	SVL of male predator	N	SVL of female predator
<i>Allolobophora caliginosa</i> (earthworm)	60	225–666 392.5 $\pm$ 11.7	88	226–666 432.1 $\pm$ 10.5
<i>Rana blairi</i>	47	411–610 522.3 $\pm$ 9.5	54	363–780 602.9 $\pm$ 13.3
<i>Rana catesbeiana</i>	7	419–582 487.4 $\pm$ 23.4	13	531–834 637.8 $\pm$ 32.7
<i>Rana</i> sp.	1	497 —	8	294–630 554.9 $\pm$ 46.8
<i>Bufo americanus</i>	5	368–596 458.0 $\pm$ 52.8	13	519–745 638.5 $\pm$ 52.9
<i>Bufo woodhousii</i>	5	459–578 432.6 $\pm$ 40.1	6	488–673 616.7 $\pm$ 40.4
<i>Hyla chrysoscelis</i>	5	243–596 426.6 $\pm$ 63.9	9	374–653 571.7 $\pm$ 30.5
<i>Acris crepitans</i>	7	228–580 413.7 $\pm$ 55.2	10	240–712 480.6 $\pm$ 59.8
<i>Pseudacris triseriata</i>	2	383–406 394.0	4	303–688 487.3 $\pm$ 96.0
<i>Microtus ochrogaster</i>	—	—	17	585–810 691.1 $\pm$ 23.6
<i>Peromyscus leucopus</i>	—	—	8	510–850 647.3 $\pm$ 44.1
<i>Reithrodontomys megalotis</i>	—	—	5	565–783 637.4 $\pm$ 37.9

\*Prey species with few records (sex and SVL of snake predator in parentheses): *Cryptotis parva* (♀, 615), *Synaptomys cooperi* (♀, 648), *Cardinalis cardinalis* (♀, 713), *Melospiza lincolni* (♀, 520). Unidentified bird (♀, 634), *Diadophis punctatus* (♀, 520), *Gastrophryne olivacea* (♀, 600), *Deroceras laeve* (♀, 303).

than half grown. Toads (*Bufo*) were taken about half as often as frogs (*Rana*), and several of those eaten, especially of the smaller *B. americanus*, were adults. Of the tree frogs (*Hyla chrysoscelis*) eaten, several had been taken by snakes found at the hilltop rock outcrops where the snakes hibernate. Perhaps the frogs also had come to these places in search of hibernacula.

In a total of 375 prey animals, most were amphibians (8 kinds), small mammals (6 kinds) and earthworms, with an occasional bird, snake, or slug. Food of the first-year young consisted almost exclusively of earthworms, but with an occasional newly metamorphosed anuran. Of 32 small mammals eaten, 31 including all the microtines (13) were taken by adult females (510 to 850 mm SVL) and only one mammal, a harvest mouse (*Reithrodontomys*) was eaten by an adult male (490 mm SVL). Frogs (*Rana*) and toads (*Bufo*) were eaten chiefly by the adult snakes, especially by females. It should be emphasized that mammals, although too bulky to be ingested by males and immatures, are regularly eaten by adult females and constitute an important resource for the developing embryos.

## DISCUSSION

The widespread occurrence of *Thamnophis sirtalis parietalis* is evidence of its plasticity and ability to thrive under diverse conditions. In recent decades, the snake dens of Manitoba Canada, have attracted much attention. There, field studies of far northern representatives of *T. s. parietalis* by Aleksiuk (1976), Aleksiuk and Stewart (1971), Crews et al. (1988), Gregory (1974), Joy and Crews (1988), Shine et al. (2001), and Shine and Mason (2001) have revealed the following traits:

1. Formation of huge denning aggregations (Joy and Crews, 1985; Crews et al., 1984); thousands of snakes hibernate together in deep limestone sinks.

2. Formation of massive mating aggregations at, or near, the hibernacula, as recently emergent males pile up, sometimes by the hundreds, to court emerging females (Gregory, 1977).

3. Presence of "she-males" in mating aggregations (Shine and Mason, 2001); these are the most recently emerged males, weak and debilitated from their long sojourn underground, but possessing the ability to produce pheromones like those of emergent females that are highly attractive to males (Shine et al., 2001). Within a time-span as short as one day such males lose much of their attractiveness but gain in strength and vigor.

4. Massive mortality at and near the dens (Shine et al., 2001). Predators, including crows, kill many, but much larger numbers are victims of their own social system. The pile ups that occur in mating aggregations may suffocate hundreds of the participants. Mortality is selective; males that are eliminated tend to be the smallest, thinnest, and weakest of those participating, and their deaths may benefit the population at large. However, the females killed tend to be the largest and heaviest, as these are the most attractive and summon the largest retinues of males.

5) Long distance dispersal (up to 20 km) from the dens, as the emergent snakes scatter to exploit extensive marshlands in the region of the dens, where they feed on a variety of marshland animals, notably the wood frog, *Rana sylvatica* (Gregory and Stewart, 1975).

It must be realized that these combined traits are not characteristic of the subspecies *T. s. parietalis* but, instead, result from the unique selective pressures generated by the environment near the northern edge of the range. None of the behaviors described above has been observed in the red-sided garter snakes of northeastern Kansas, thereby indicating widely divergent responses to contrasting environments. No comparison of morphology or color pattern has yet been made between the Kansas population of *T. s. parietalis* and that of Manitoba.

The longitudinally striped pattern is adaptive in that it conceals motion as the snake moves through dense vegetation. It is significant that adult females, larger and more

aggressive than male counterparts, are somewhat more likely to have red in the pattern and to respond to confrontation with semantic display, whereas males are less aggressive and more inclined to escape and to seek concealment.

Shine (1991) pointed out that *Thamnophis* are unusual

among snakes for their marked sexual dimorphism in head size, with the females having relatively larger heads. Mammals, although too bulky to be ingested by males and immatures, are eaten regularly by adult females. This dietary difference helps to explain how this sexual dimorphism is maintained.

#### LITERATURE CITED

- Aleksiuk, M. 1976. Reptilian hibernation. Evidence of adaptive strategies in *Thamnophis sirtalis parietalis*. *Copeia* 1976:170-178.
- Aleksiuk, M., and K. Stewart. 1971. Seasonal change in the body composition of the garter snake (*Thamnophis sirtalis parietalis*) at northern latitudes. *Ecology* 52:485-490.
- Crews, D., M. Diamond, R. Tokarz, B. Camazine, and W. Garstka. 1984. Hormone independence of male sexual behavior in a garter snake. *Hormonal Behavior* 18:29-41.
- Crews, D., V. Hingorani, and R. J. Nelson. 1988. Role of the pineal gland in the control of annual reproductive, behavioral, and physiological cycles in the red-sided garter snake (*Thamnophis sirtalis parietalis*). *Journal of Biological Rhythms* 3:293-302.
- Fitch, H. S. 1941. Geographic variation in the garter snakes of the species *Thamnophis sirtalis* in the Pacific Coast Region of North America. *American Midland Naturalist* 26:570-592.
- Fitch, H. S. 1965. An ecological study of the garter snake, *Thamnophis sirtalis*. University of Kansas Museum of Natural History 15:493-564.
- Fitch, H. S. 1980. *Thamnophis sirtalis*. Catalog of American Amphibians and Reptiles 279:1-4.
- Fitch, H. S. 1999. A Kansas Snake Community: Composition and Changes over Fifty Years. Malabar, Florida: Krieger Publishing Company, xi + 165 pp.
- Gregory, P. T. 1974. Patterns of spring emergence of the red-sided garter snake (*Thamnophis sirtalis parietalis*) in the Interlake region of Manitoba. *Canadian Journal of Zoology* 52:1063-1069.
- Gregory, P. T. 1977. Life history parameters of the red-sided garter snake (*Thamnophis sirtalis parietalis*) in an extreme environment, the Interlake region of Manitoba. National Museum of Canada, Publications in Zoology 13:1-44.
- Gregory, P. T., and K. W. Stewart. 1975. Long-distance dispersal and feeding strategy of the red-sided garter snake (*Thamnophis sirtalis parietalis*) in the Interlake of Manitoba. *Canadian Journal of Zoology* 53:238-245.
- Joy, J. E., and D. Crews. 1985. Social dynamics of group courtship behavior in male red-sided garter snakes (*Thamnophis sirtalis parietalis*). *Journal of Comparative Psychology* 99:145-149.
- Rossman, D. A., N. B. Ford, and R. A. Seigel. 1996. The garter snakes: evolution and ecology. Norman, Oklahoma: University of Oklahoma Press, xx + 331 pp.
- Ruthven, A. G. 1908. Variation and genetic relationships of the garter-snakes. *Bulletin of the United States National Museum* 61, xii + 201 pp.
- Shine, R. 1991. Why do larger snakes eat larger prey items? *Functional Ecology*, 5:491-502.
- Shine, R., M. P. LeMaster, L. T. Moore, M. M. Olsson, and R. T. Mason. 2001. Bumpus in the snake den: effects of sex, size and body condition on mortality of red-sided garter snakes. *Evolution* 55:598-604.
- Shine, R., and R. Mason. 2001. Serpentine cross-dressers. *Natural History Magazine*. February 2001:59-61.





## PUBLICATIONS OF THE NATURAL HISTORY MUSEUM, THE UNIVERSITY OF KANSAS

The University of Kansas Publications, Museum of Natural History, beginning with Volume 1 in 1946, was discontinued with Volume 20 in 1971. Shorter research papers formerly published in the above series were published as The University of Kansas Natural History Museum Occasional Papers until Number 180 in December 1996. The Miscellaneous Publications of The University of Kansas Natural History Museum began with Number 1 in 1946 and ended with Number 68 in February 1996. Monographs of The University of Kansas Natural History Museum were initiated in 1970 and discontinued with Number 8 in 1992. The University of Kansas Science Bulletin, beginning with Volume 1 in 1902, was discontinued with Volume 55 in 1996. The foregoing publication series are now combined in a new series entitled Scientific Papers, Natural History Museum, The University of Kansas, begun with Number 1 in 1997. Special Publications began in 1976 and continue as an outlet for longer contributions and are available by purchase only. All manuscripts are subject to critical review by intra- and extramural specialists; final acceptance is at the discretion of the editor.

The publication is printed on acid-free paper. Publications are composed using Microsoft Word® and Adobe PageMaker® on a Macintosh computer and are printed by The University of Kansas Printing Services.

Institutional libraries interested in exchanging publications may obtain the Scientific Papers, Natural History Museum, The University of Kansas, by addressing the Exchange Librarian, The University of Kansas Libraries, Lawrence, Kansas 66045-2800, USA. Available back issues of The University of Kansas Science Bulletin may be purchased from the Library Sales Section, Retrieval Services Department, The University of Kansas Libraries, Lawrence, Kansas 66045-2800, USA. Available issues of former publication series, Scientific Papers, and Special Publications of the Natural History Museum can be purchased from the Office of Publications, Natural History Museum, The University of Kansas, Lawrence, Kansas 66045-2454, USA. Purchasing information can be obtained by calling (785) 864-4450, fax (785) 864-5335, or e-mail ([kunhm@ukans.edu](mailto:kunhm@ukans.edu)). VISA and MasterCard accepted; include expiration date.

SERIES EDITOR: William E. Duellman

PRINTED BY  
THE UNIVERSITY OF KANSAS PRINTING SERVICES  
LAWRENCE, KANSAS